Triassic *Kykloxylon* wood (Umkomasiaceae, Gymnospermopsida) from Skinner Ridge, northern Victoria Land, East Antarctica

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ABSTRACT

During the first Korea Antarctic Geological Expedition (KAGEX I, 2013/2014), fossil wood was collected from the Triassic fluvial deposits of the Beacon Supergroup at Skinner Ridge in northern Victoria Land, Antarctica. The material is coalified and partially silicified; most specimens are slightly compressed due to burial compaction. In spite of this imperfect preservation, anatomical features of both the xylem and the pith could be observed in some specimens. The xylem displays prominent growth rings and usually araucarioid or somewhat mixed-type radial pitting with some abnormal rings partly composed of parenchymatous tissues. Some specimens also have a wood cylinder that is divided radially by parenchymatous zones. These anatomical features indicate a systematic affinity with *Kykloxylon* Mey.-Berth., T.N.Taylor et Ed.L.Taylor, a characteristic wood type of the Umkomaciaceae, which flourished throughout Gondwana during the Triassic. The *Kykloxylon* specimens in this study represent the only wood fossil taxon in the Triassic of Victoria Land, except for a dubious report of *Antarcticoxylon* Seward in 1914. This may indicate a low diversity of Triassic wood fossils in this area, as in other parts of Antarctica. On the contrary, diverse other gymnosperm organs are known to occur in the Triassic of Antarctica. This low diversity of wood taxa compared to the various plant organs in the Triassic of Antarctica is remarkable. We hypothesize three major reasons for this: 1) the overall structural uniformity of gymnosperm wood compared to other vegetative and especially reproductive organ diversity; 2) the overwhelming dominance of corystosperm plants, with a minor component of voltzialean conifers in the canopy-forming forest vegetation during the Triassic in Antarctica; and 3) the very few systematic studies of fossil wood compared to other plant macrofossils.

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1. Introduction

Numerous plant-fossil assemblages in the extensively exposed Triassic deposits of Antarctica have provided a wealth of information on the early Mesozoic vegetation of southern Gondwana (e.g., Barrett et al., 1986; Collinson et al., 1986, 1994; Escapa et al., 2011; Cantrill and Poole, 2012 and references therein). Although some possible occurrences of Triassic plant fossils have been reported from the Antarctic Peninsula (e.g., Lacey and Lucas, 1981; Barale et al., 1994), most Triassic plant fossils are known from the Central Transantarctic Mountains, southern Victoria Land, northern Victoria Land, and—to a lesser extent—the Prince Charles

Mountains. Of particular importance are the perminieralized peat deposits of the Fremouw Formation in the Central Transantarctic Mountains, which contain a rich and diverse assemblage of structurally preserved plant remains, including sphenophytes (Osborn and Taylor, 1989; Osborn et al., 2000; Ryberg et al., 2008), ferns (e.g., Schopf, 1978; Millay and Taylor, 1990; Phipps et al., 2000; Rothwell et al., 2002; Klavins et al., 2004), seed ferns (Pigg, 1990; Meyer-Berthaud et al., 1992, 1993; Osborn and Taylor, 1993; Taylor et al., 1994; Yao et al., 1995; Klavins et al., 2002; Bomfleur et al., 2014c), cycads (e.g., Smoot et al., 1985; Klavins et al., 2003; Hermsen et al., 2007a), and conifers (e.g., Mey.-Berth. et T.N.Taylor, 1991; Yao et al., 1997; Axsmith et al., 1998; Hermsen et al., 2007b). The systematic affinities and palaeoenvironmental significance of fossil wood associated with these peat deposits in the Central Transantarctic have received considerable attention (Mey.-Berth. et T.N.Taylor,
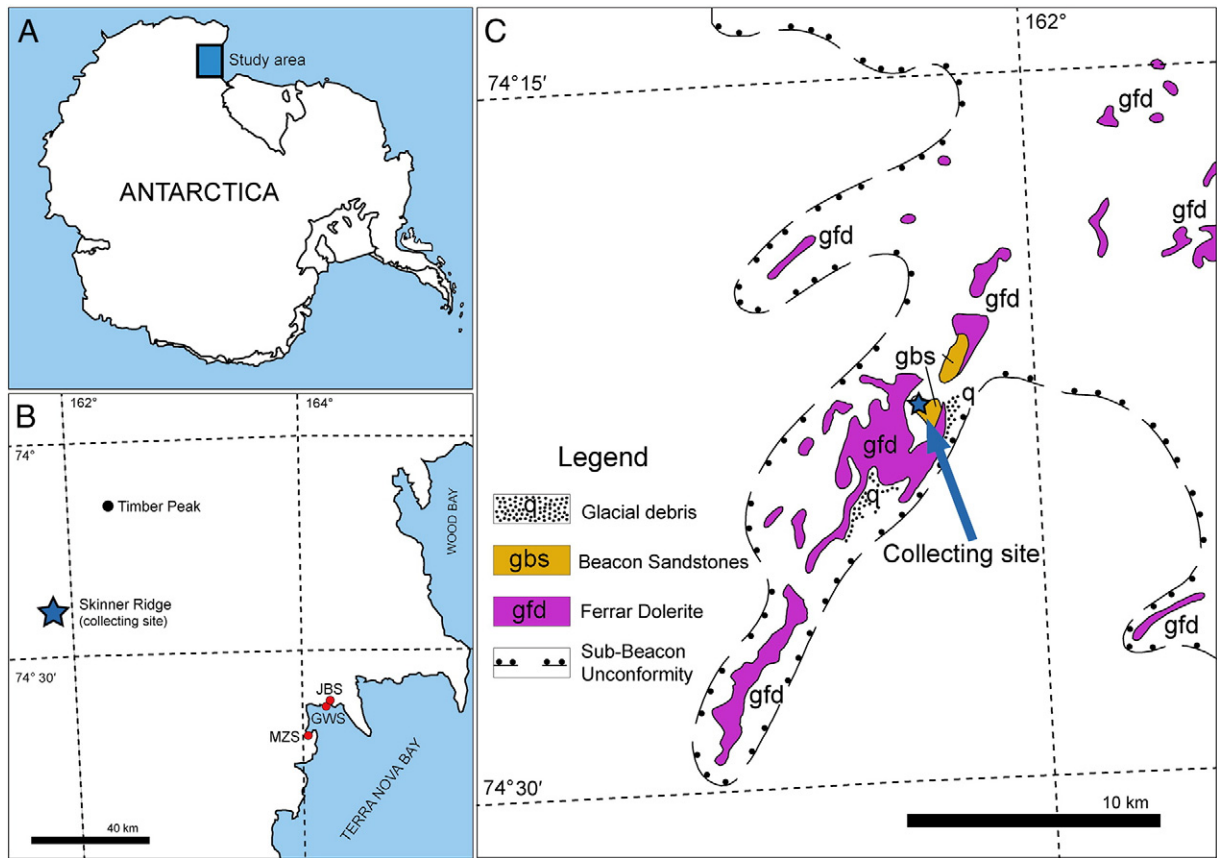
Fig. 1. Geographic and geological map showing the study area and collecting site. (A) Geographic map of Antarctica with study area indicated by blue rectangle. (B) Geographic map of the Eisenhower Range area in northern Victoria Land in Antarctica with collecting site indicated by blue star (JBS=Jang Bogo Station, Korea; GWS=Gondwana Station, Germany; MZS=Mario Zucchelli Station, Italy). (C) Geological map of the Skinner Ridge area with collecting site indicated by blue arrow (from GANOVEX Team, 1987).

1991; Taylor, 1992; Meyer-Berthaud et al., 1992, 1993; Del Fueyo et al., 1995; Cúneo et al., 2003; Ryberg and Taylor, 2007; Decombeix et al., 2010a, 2014). However, it is noticeable that the diversity of gymnosperm wood taxa is significantly lower than that of other gymnosperm plant organs in the associated peat deposits and compression floras.

In the course of the 9th German Antarctic North Victoria Land Expedition (GANOVEX IX; 2005/2006), new and well-preserved Triassic plant-fossil assemblages were found also in northern Victoria Land (Bomfleur et al., 2007, 2011a). However, the study of these new Triassic fossil deposits has focused almost exclusively on compression remains (Bomfleur et al., 2007, 2011a; Bomfleur and Kerp, 2010), and the wood fossils, which may provide information on the Triassic wood diversity in northern Victoria Land, have remained unstudied. Here, we present a systematic description of fossil wood from northern Victoria Land that was collected during the first Korea Antarctic

Geological Expedition (KAGEX I; 2013/2014) and provide possible explanations for the low diversity of gymnosperm wood in the Antarctic Triassic flora.

2. Geological setting, materials and methods

The material was collected from an isolated exposure of the Beacon Supergroup at Skinner Ridge in the western Eisenhower Range, northern Victoria Land, Antarctica (S74°21′45.53″, E161°51′15.99″) (Fig. 1). The stratigraphy of Beacon Supergroup deposits in this region is poorly resolved due to the poor accessibility and the lack of continuous exposures. The precise stratigraphic relationships between the Palaeozoic deposits in the south and east of the Eisenhower Range and the occurrences of Triassic deposits at Timber Peak and Skinner Ridge remain uncertain. Nevertheless, it has traditionally been assumed that all sedimentary deposits intercalate between the crystalline basement
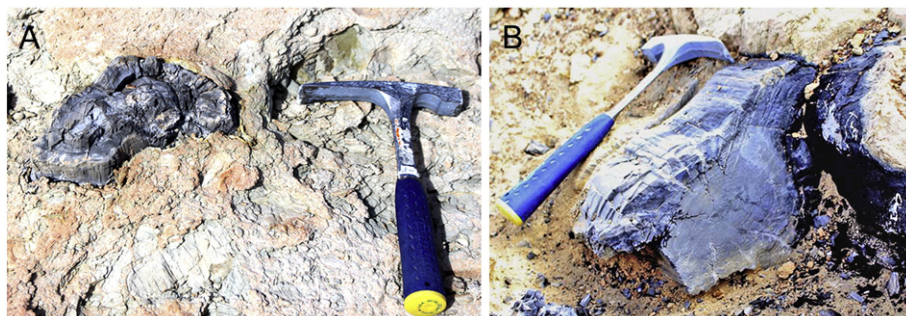

Fig. 2. Field images showing pieces of fossil wood embedded in the sandstone. (A) Upright-buried stem (KOPRIF 20001). (B) Horizontally embedded fossil wood (KOPRIF 20008).
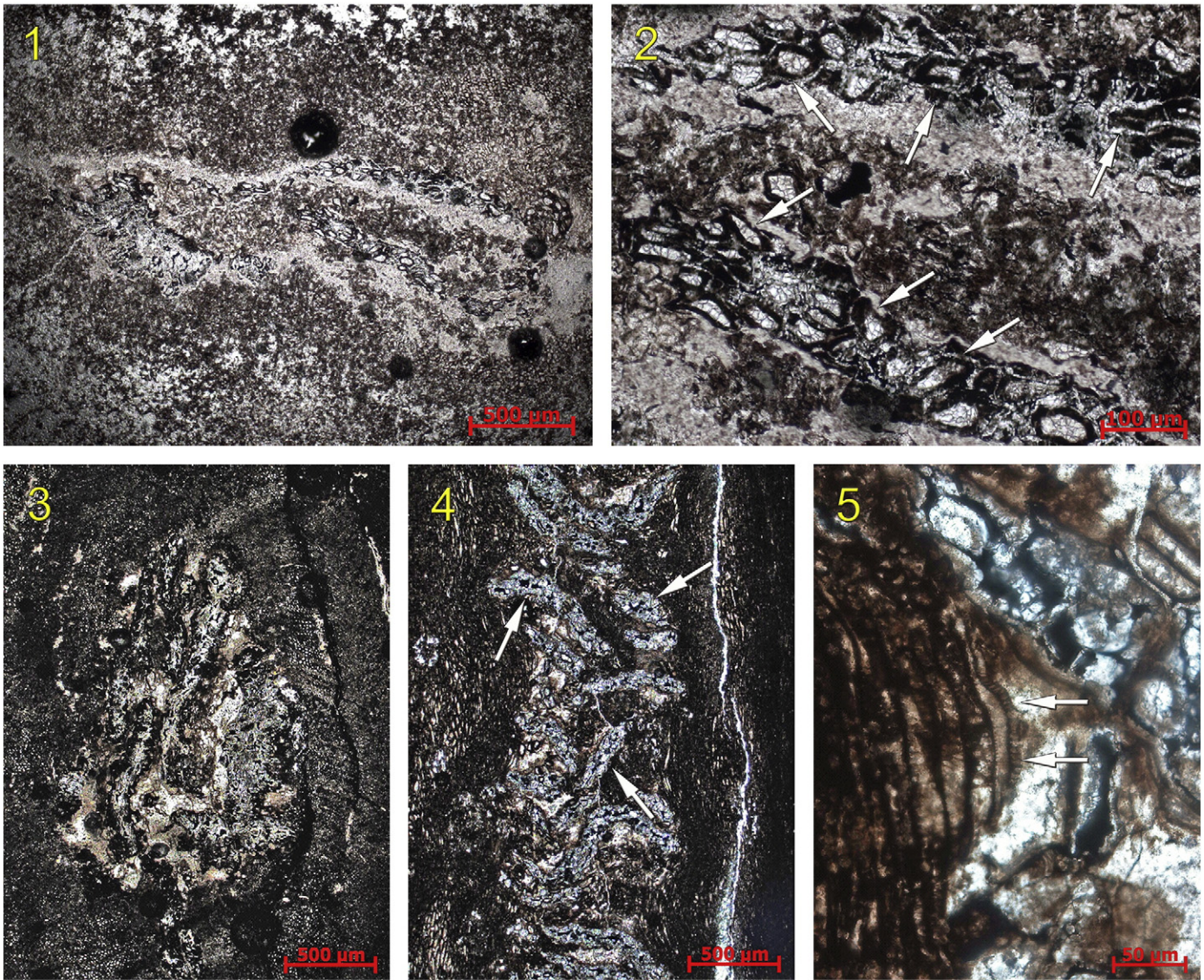
Plate I. Microphotographs showing the anatomical features of pith and primary xylem of *Kykloxylon fremouwense* from Skinner Ridge. (1) Transverse section showing the heterogeneous pith (specimen no. KOPRIF 20001). (2) Detail of the pith showing the clusters of thick-walled sclerenchymatous cells (arrows; specimen no. KOPRIF 2001). (3) Transverse section showing the heterogeneous pith (specimen no. KOPRIF 20008). (4) Longitudinal section showing the clusters of thick-walled sclerenchymatous cells with no particular organization (arrows; specimen no. KOPRIF 20001). (5) Detail of the primary xylem showing the helical wall thickenings (arrows; specimen no. KOPRIF 20001).

and (within) the Ferrar sills in the Eisenhower Range area, and belong to the Triassic to Early Jurassic Section Peak Formation (e.g., Collinson et al., 1986; Casnedi and Di Giulio, 1999; Schöner et al., 2011; Elsner et al., 2013). Recent palynological analyses, however, have shown that the basal, overall coarser-grained and more arkosic part of the sedimentary succession represents a previously unidentified Permian unit (Bomfleur et al., 2014a, 2014b), which locally overlies thin lenses of diamictite that may be late Carboniferous–earliest Permian glacial tillites (Schöner et al., 2011; Bomfleur et al., 2014a, 2014b).

At Skinner Ridge, fossil wood is coalified to partly silicified, and occurs in the form of either upright-buried stems up to 30 cm in diameter or transported and more or less compressed stem segments. One particularly well-preserved trunk fossil has been declared Antarctic Monument by the Italian Antarctic Research Programme

(PNRA). We collected eight samples of slightly compressed stem fragments from beds of massive sandstone (Fig. 2). Three thin-section (transverse, radial, and tangential) slides were prepared from each specimen for anatomical study according to the method described by Hass and Rowe (1999). The slides were studied using a Zeiss Axiophot light microscope and images were taken with an AxioCam HRc. In addition, acetate peels were prepared after etching in 48% hydrofluoric acid (HF) following the method detailed by Galtier and Phillips (1999); selected peels were scanned using a HP Scanjet 5590 at 1200 DPI. Conventional adjustments of sharpness, brightness, contrast, and saturation of the digital images were done using Adobe Photoshop CS5. All specimens, slides, and peels are currently housed in the collection of the Korea Polar Research Institute, under the accession numbers KOPRIF 20001–20008.

Plate II. Microphotographs showing the anatomical features of the secondary xylem of *Kykloxylon fremouwense* at Skinner Ridge (specimen no. KOPRIF 20001). (1) Transverse section showing the distinct growth ring and tracheids in radial row. (2) Detail of growth ring showing the compressed and crushed late wood. (3) Radial section showing the unusual parenchymatous tissues in tangential direction (arrows). (4) Radial section showing contiguous bordered pits on the radial walls of tracheids. (5) Radial section showing partly separated bordered pits on the radial walls of tracheids. (6) Radial section showing alternate or subopposite bordered pits on the radial walls of tracheids. (7) Radial section showing several small araucarioid-type cross-field pits. (8) Tangential section showing uniseriate rays. (9) Detail of uniseriate rays with low height.
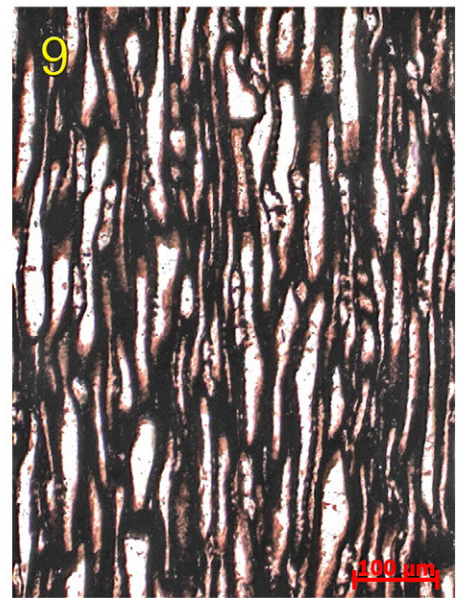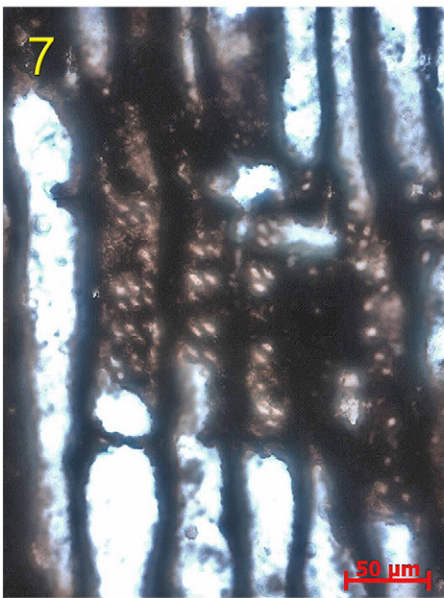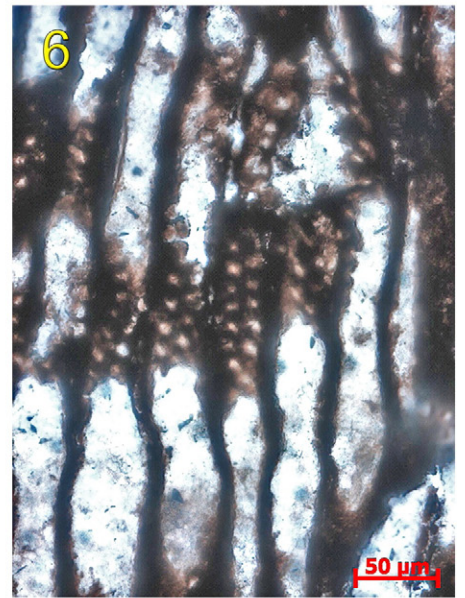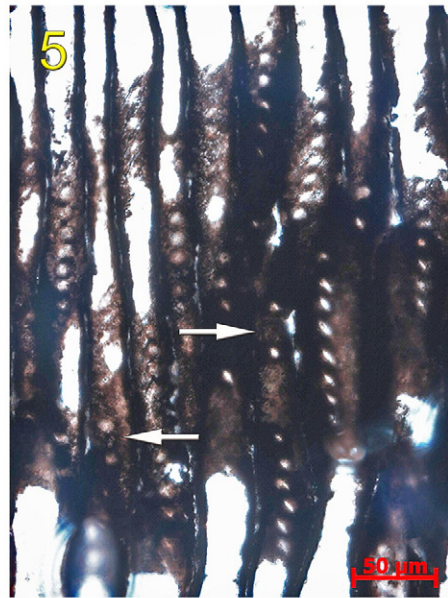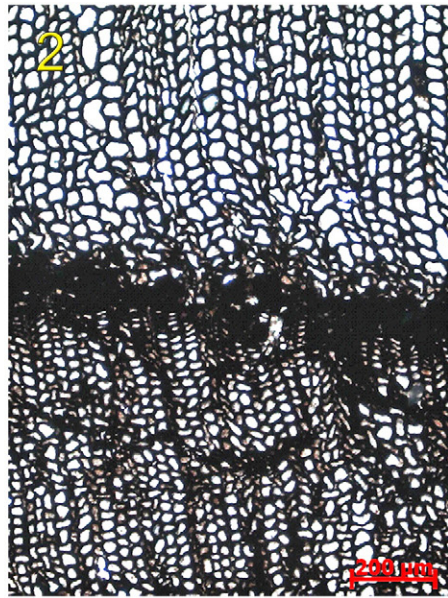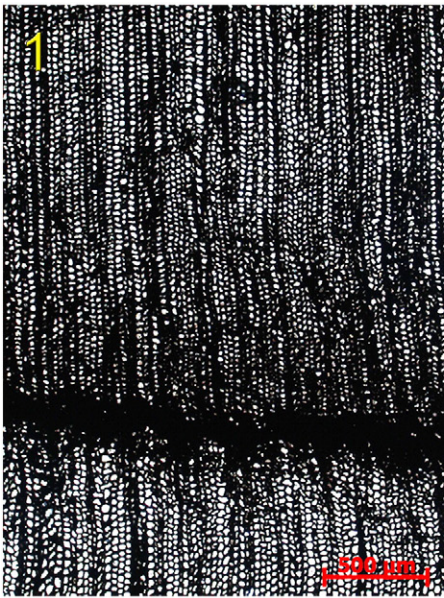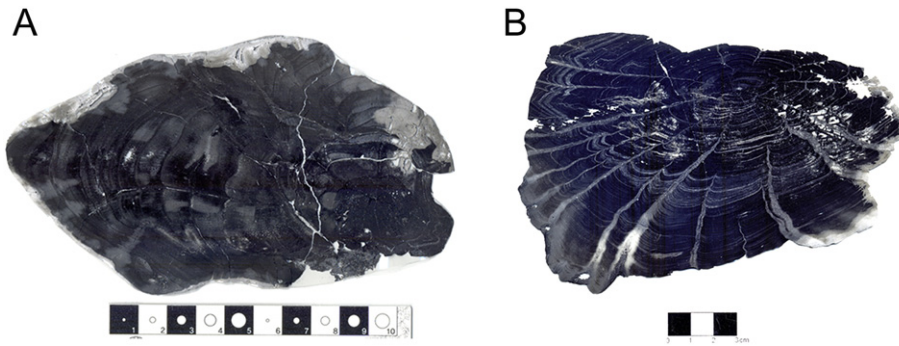
Fig. 3. Scanned images showing the acetate peels of *Kykloxylon fremouwense* from Skinner Ridge. (A) The acetate peel of specimen no. KOPRIF 20001 (one square = 1 cm²). (B) The acetate peel of specimen no. KOPRIF 20008 clearly showing the unusual parenchymatous tissue bands in radial and tangential direction (one square = 1 cm²).

3. Results

Among the eight specimens (KOPRIF 20001–20008), KOPRIF 20001 is best preserved and has, therefore, yielded most anatomical information for the systematic description. Specimen KOPRIF 20008, despite its poorer preservation, is identified as belonging to the same taxon as KOPRIF 20001 because it shares the same pith composition and the presence of similar unusual parenchymatous tissues in the wood. The other specimens, i.e., KOPRIF 20002–20007, could not be identified to generic level clearly due to their poor preservation.

Class: Gymnospermopsida Stewart et G.W.Rothwell 1993
Order: Corystospermales Petriella 1981
Family: Umkomasiaceae Petriella 1981
Genus: *Kykloxylon* Mey.-Berth., T.N.Taylor et Ed.L.Taylor 1993
Type species: *Kykloxylon fremouwense* Mey.-Berth., T.N.Taylor et Ed.L.Taylor 1993
Kykloxylon fremouwense (Plates I, II; Fig. 3)
1995 *Jeffersonioxylon gordonense* Del Fueyo, Ed.L.Taylor, T.N.Taylor et Cúneo, p. 113, Figs. 1–4; p. 116, Figs. 5–9; p. 117, Figs. 10–15.
2014 *Kykloxylon gordonense* (Del Fueyo, Ed.L.Taylor, T.N.Taylor et Cúneo) Decombeix, Bomfleur, Ed.L.Taylor et T.N.Taylor, p. 27, Plate II, 11.
Material: Specimens KOPRIF 20001 and 20008.
Description: 1) Pith and primary xylem — The pith is narrow, about 2.4–2.6 mm in diameter (Plate I, 1 & 3). It is compressed and oval. The pith tissues are heterogeneous, composed of parenchyma and clusters of sclerenchymatous cells (Plate I, 2). These clusters are distributed along the periphery of the pith in some cases, but usually without any notable arrangement (Plate I, 4). The sclereids are somewhat rounded or polygonal with thick walls (Plate I, 2). Most parenchyma in the pith is difficult to identify because of poor preservation. Primary xylem strands are endarch and their tracheids have helical wall thickenings (Plate I, 5). No perimedullary bundles and centripetal development of secondary tissues were observed. 2) Secondary xylem — The secondary xylem is basically homoxylous, although it contains unusual parenchymatous tissues in both the radial and tangential directions. In the radial direction, the tissues transect the secondary xylem cylinder, and growth rings on both sides are curved inwardly (Fig. 3). In specimen KOPRIF 20008, this pattern is particularly prominent in the form of grayish bands (Fig. 3B). However, these grayish bands are not composed entirely of parenchymatous tissues; upon microscopic observation, parenchymatous tissues are narrow and most of the gray area is composed of the surrounding secondary xylem. In the tangential direction, the bands of unusual parenchymatous tissues, which are very similar to the "unusual rings" mentioned by Decombeix et al. (2014), are usually observed within the growth ring at the transition zone between the late wood and the early wood (Plate II, 3). In longitudinal section, they are 15–75 μm (mean 43 μm, n = 30) long (Plate II, 3). Growth rings are distinct, with 1–4 or more layers of late wood tracheids (Plate II, 1 & 2). The transition from early wood to late wood is abrupt. The rings are about

0.9–11.2 mm wide. Early wood tracheids are rounded, squarish, or polygonal in transverse section and are 19–80 × 19–63 μm (mean 35 × 32 μm, n = 70) in radial × tangential diameter (Plate II, 1 & 2). Late wood tracheids are small, usually compressed or distorted, somewhat radially flattened in transverse section and about 9–23 × 22–35 μm in radial × tangential diameter (Plate II, 2). Normal axial parenchyma and resin canals were not observed. Bordered pits are absent on tangential walls of tracheids. Rays in tangential section are usually uniseriate or rarely partly biseriate (Plate II, 8 & 9), homogenous, 1–13 cells high (mean 3, n = 34), and consist entirely of parenchyma cells. Ray cells are oval, oblong, or circular in tangential section and 13–22 × 22–35 μm (mean 17 × 28 μm, n = 25) in tangential × longitudinal diameter (Plate II, 8 & 9). They have smooth end walls in radial section. Bordered pits on the radial walls of tracheids are usually contiguous and slightly flattened or in a few cases somewhat separated with a circular outline (Plate II, 4 & 5). The pits are usually ordered in one or two, rarely three rows and are approximately 12–21 μm in diameter. When in two or more rows they are alternate or subopposite (Plate II, 6). The apertures of the pits are slit-like or oval in outline. Several small pits (i.e., araucarioid-type) are present in the early wood cross-fields (Plate II, 7). They are simple, taxodioid or somewhat cupressoid in shape and arranged in one or two rows, with 1–6 pits per field (Plate II, 7). The pits are approximately 6–12 μm in diameter. Ray tracheids are absent.

Remarks and comparisons: Several Triassic pycnoxylic homoxylous wood taxa have been reported from Antarctica: *Antarcticoxylon* Seward (1914), *Kykloxylon*, *Jeffersonioxylon* Del Fueyo, Ed.L.Taylor, T.N.Taylor et Cúneo (1995), *Notophytum* Mey.-Berth. et T.N.Taylor (1991), *Rudixylon* Bomfleur, Decombeix, Schwendemann, Escapa, Ed.L.Taylor, T.N.Taylor et McLoughlin (2014c), and *Rhexoxylon* Bancroft (1913; Taylor, 1992) (see Table 1).

Meyer-Berthaud et al. (1992) revealed the relationship between the leaf fossil genus *Dicroidium* (Corystospermales) and the petrified stems occurring at Fremouw Peak in the Central Transantarctic Mountains. Subsequently, Meyer-Berthaud et al. (1993) confirmed that they both belonged to the same tree and the stem part was then named *Kykloxylon fremouwense*. Recently, Decombeix et al. (2014) studied these corystosperm trees based on newly discovered *Kykloxylon* petrified trunks and young stems from Fremouw Peak. Fossil wood from Skinner Ridge agrees closely in anatomical features with *Kykloxylon* trunks from Fremouw Peak. They have dilatation parenchyma tissues in both tangential and radial directions, an unequal cambium activity, no centripetal secondary xylem, endarch primary xylem maturation, similar ray height, cross-field pit numbers, tracheid radial pit arrangements, pith composition, and general size (Decombeix et al., 2014). The only difference could be the cross-field pits; those of *K. fremouwense* from Fremouw Peak are mainly simple (see Decombeix et al., 2014, p. 32), whereas the specimens in this study commonly have simple, taxodioid or cupressoid type cross-field pits. However, at least one *Kykloxylon* specimen (Decombeix et al., 2010a, Plate I, 8, arrowheads) also displays somewhat cupressoid oculipores, and, therefore, this character could be

Table 1
Comparison of anatomical characters between Triassic fossil wood types from Antarctica and corystosperm stems from South Africa and South America (modified from Decombeix et al., 2014).

	Antarcticoxylon	*Notophytum*	*Rudixylon*	*Rhexoxylon*	*Tranquiloxylon*	*Cuneumxylon*	*Elchaxylon*	*Kykloxylon*
MD	7.6 cm	0.5–20 cm	1–3 mm	7–80 cm	26–30 cm	30–90 cm	5–58 cm	1.5–60 cm
PS	2–3 mm	1–2.5 mm	0.5–1.5 mm	8–60 mm	7 × 33 mm (compressed)	2–3 mm	2 × 12 mm (compressed)	0.5–4 mm
PCT	Heterogeneous	Heterogeneous	Homogeneous	Heterogeneous	Not reported	Heterogeneous	Homogeneous	Heterogeneous
PMB	–	–	–	+ (except *R. cortaderitaense*)	–	–	–	–
PXM	Endarch	Endarch	Endarch	Mesarch	Endarch	Endarch	Mesarch	Endarch
CXM	–	–	–	+	–	–	+	–
UPTRTD	+	–	–	+	+	+	–	+
AP	–	+	Not reported	+, –	Not reported	Not reported	+	–
TRP	1–2	1–(2)	1–2	1–2	1–2	1–2	1–2	1–2–(3) rows
ATRP	Alternate	Alternate, opposite	Alternate	Alternate, opposite	Alternate, subopposite	Alternate, subopposite	Alternate, opposite	Alternate, opposite or subopposite
CFP	Not reported	1–2–(4) large simple pits	Not reported	1–3 large or small pits	Several simple pits	2–13 small pits	1–(2–3) simple pits	1–9 small pits
RW	Uniseriate	Uniseriate	Uniseriate	Uniseriate	Uniseriate, biseriate	Uniseriate	Uniseriate	Uniseriate, partly biseriate
RH	1–24 cells	1–7 cells	1–25 cells	1–7–20 cells	2–13 cells	1–15 cells	1–20 cells	1–13 cells
Distribution	Antarctica	Antarctica	Antarctica	South Africa, South America	South America	South America	South America	Antarctica
References	Seward (1914)	Mey.-Berth. et T.N.Taylor (1991)	Bomfleur et al. (2014c)	Bancroft (1913), Walton (1923), Archangelsky and Brett (1961), Herbst and Lutz (1988), Artabe et al. (1999), Bodnar (2008)	Herbst and Lutz (1995)	Artabe and Brea (2003)	Artabe and Zamuner (2007)	Meyer-Berthaud et al. (1993), Del Fueyo et al. (1995), Decombeix et al. (2014); this study

MD: Maximum diameter, PS: Pith size, PCT: Pith component type, PMB: Peri-medullary bundles, PXM: Primary xylem maturation, CSX: Centripetal secondary xylem, UPTRTD: Unusual parenchymatous tissues in radial and tangential direction, AP: Axial parenchyma, TRP: Tracheid radial pitting, ATRP: Arrangement of tracheid radial pitting, CFP: Cross-field pitting, RW: Ray width, RH: Ray height, +: present, –: absent.

Table 2
List of Triassic gymnosperm fossil plant species documented in Antarctica (CTM=central Transantarctic Mountains, SVL=southern Victoria Land, NVL=northern Victoria Land, PCM=Prince Charles Mountains, LSI=Livingston Island).

Species name	Organ type	Locality	References
Antarcticoxylon priestley	Pycnoxylic wood	NVL	Seward (1914)
Antarcticycas schopfii	Manoxylic wood, leaf, root	CTM	Smoot et al. (1985), Millay et al. (1987), Hermsen et al. (2006, 2009)
Baiera sp.	Leaf	SVL	Rigby (1985)
Caytonia sp.	Leaf	LSI	Barale et al. (1994)
Czekanowskia-like foliage	Leaf	CTM	Escapa et al. (2011)
Dejerseya lobata	Leaf	CTM	Bomfleur et al. (2011b)
Dejerseya sp.	Leaf	NVL	Escapa et al. (2011)
Delemaya spinulosa	Pollen organ	CTM	Klavins et al. (2003)
Dicroidium coriaceum	Leaf	SVL, NVL	Bomfleur and Kerp (2010), Chatterjee et al. (2013)
D. crassinerve	Leaf	CTM, SVL, NVL, LSI	Barale et al. (1994), Cúneo et al. (2003), Bomfleur and Kerp (2010), Chatterjee et al. (2013)
D. dubium	Leaf	CTM, NVL, PCM, LSI	Rigby (1985), Taylor et al. (1992), Boucher et al. (1993), Barale et al. (1994), Bomfleur and Kerp (2010)
D. dutoitii	Leaf	CTM, SVL	Townrow (1967), Taylor et al. (1990), Boucher et al. (1995)
D. elongatum	Leaf	CTM, SVL, NVL, LSI	Townrow (1967), Gabites (1985), Rigby (1985), Barale et al. (1994), Bomfleur and Kerp (2010)
D. feistmantelii	Leaf	CTM, SVL	Townrow (1967), Rigby and Schopf (1969)
D. fremouwense	Leaf	CTM, SVL	Pigg (1990), Chatterjee et al. (2013)
D. lancifolium	Leaf	CTM	Gabites (1985), Taylor et al. (1992), Boucher et al. (1993), Bomfleur et al. (2011b)
D. odontopteroides	Leaf	CTM, SVL, NVL, LSI	Townrow (1967), Gabites (1985), Rigby (1985), Rigby and Schopf (1969), Taylor et al. (1990, 1992), Boucher et al. (1993, 1995), Barale et al. (1994), Axsmith et al. (2000), Retallack (2005), Bomfleur and Kerp (2010), Chatterjee et al. (2013)
D. spinifolium	Leaf	SVL, NVL	Boucher et al. (1995), Bomfleur and Kerp (2010)
D. stelznerianum	Leaf	CTM, PCM	Gabites (1985), Webb and Fielding (1993), Cantrill et al. (1995), Cúneo et al. (2003)
D. trilobitum	Leaf	SVL	Townrow (1967), Gabites (1985), Boucher et al. (1995)
D. zuberi	Leaf	CTM, SVL, PCM	Gabites (1985), Rigby (1985), Webb and Fielding (1993), Cantrill et al. (1995), McLoughlin et al. (1997), Retallack (2005)
Dicroidium sp. A	Leaf	NVL	Bomfleur and Kerp (2010)
Dicroidium sp.	Leaf	SVL, LSI	Plumstead (1962), Barale et al. (1994)
Diplasiophyllum acutum	Leaf	CTM, SVL	Townrow (1967)
Dordrechtites arcanus	Ovulate organ	CTM	Bergene et al. (2013)
Elatocladus sp.	Leaf	LSI	Barale et al. (1994)
Heidiphyllum elongatum	Leaf	CTM, SVL, NVL, PCM	McLoughlin et al. (1997), Bomfleur and Kerp (2010), Bomfleur et al. (2011b, 2011c), Chatterjee et al. (2013)
Ignotospermum monilii	Ovulate organ	CTM	Perovich and Taylor (1989)
Kykloxylon fremouwense	Pycnoxylic wood	CTM, NVL	Meyer-Berthaud et al. (1992, 1993), Del Fueyo et al. (1995), Cúneo et al. (2003), Decombeix et al. (2014), this study

Table 2 (*continued*)

Species name	Organ type	Locality	References
Leastrobus fallae	Pollen organ	CTM	Hermsen et al. (2007b)
Lepidopteris langlohensis	Leaf	NVL	Bomfleur and Kerp (2010)
L. stormbergensis	Leaf	CTM	Escapa et al. (2011)
Lepidopteris sp.	Leaf	PCM	McLoughlin et al. (1997)
Linguifolium spp.	Leaf	SVL, NVL, LSI	Gabites (1985), Rigby (1985), Tessensohn and Mädler (1987), Barale et al. (1994), Bomfleur et al. (2007)
Matatiella dejerseyi	Ovulate organ	CTM, SVL	Bomfleur et al. (2011b), Chatterjee et al. (2013)
Nilssonia sp.	Leaf	SVL	Plumstead (1962)
Notophytum krauselii	Pycnoxylic wood, leaf, root	CTM	Mey.-Berth. et T.N.Taylor (1991), Axsmith et al. (1998), Decombeix et al. (2011)
Pagiophyllum papillatus	Leaf	PCM	Cantrill et al. (1995), McLoughlin et al. (1997)
Pagiophyllum sp.	Leaf	CTM, LSI	Barale et al. (1994), Retallack (2005)
Petriellaea triangulata	Ovulate organ	CTM	Taylor et al. (1994)
Podozamites sp.	Leaf	SVL	Axsmith et al. (1995)
Probolosperma antarcticum	Ovulate organ	CTM	Decombeix et al. (2010b)
Pteruchus dubius	Pollen organ	PCM	Cantrill et al. (1995)
P. cf. *barrealensis*	Pollen organ	PCM	Webb and Fielding (1993)
P. fremouwensis	Pollen organ	CTM	Yao et al. (1995)
Pteruchus sp.	Pollen organ	CTM, SVL	Osborn and Taylor (1993), Axsmith et al. (2000), Chatterjee et al. (2013)
Rhexoxylon sp.	Pycnoxylic wood	CTM	Taylor (1992)
Rochipteris alexandriana	Leaf	SVL	Bomfleur et al. (2014c)
R. cf. *lacerate*	Leaf	CTM	Bomfleur et al. (2014c)
Rudixylon serbetianum	Pycnoxylic wood	CTM	Bomfleur et al. (2014c)
Sagenopteris sp.	Leaf	LSI	Barale et al. (1994)
Sphenobaiera schenkii	Leaf	CTM, SVL	Escapa et al. (2011)
Sphenobaiera sp.	Leaf	CTM, LSI	Barale et al. (1994), Escapa et al. (2011)
Switzianthus sp.	Pollen organ	CTM, SVL	Bomfleur et al. (2011c)
Taeniopteris sp.	Leaf	CTM, SVL	Townrow (1967), Axsmith et al. (2000)
Telemachus aequata	Ovulate organ	CTM	Yao et al. (1997), Schwendemann et al. (2010)
T. antarcticus	Ovulate organ	SVL	Escapa et al. (2010)
T. elongatus	Ovulate organ	CTM, SVL	Yao et al. (1993), Axsmith et al. (1995), Escapa et al. (2010)
Townrovia polaris	Pollen organ	CTM, SVL	Bomfleur et al. (2011b), Chatterjee et al. (2013)
Umkomasia resinosa	Ovulate organ	CTM	Klavins et al. (2002)
U. uniramia	Ovulate organ	CTM	Axsmith et al. (2000)
Voltziopsis africana	Leaf	CTM	Retallack (2005)
Yelchophyllum omegapetiolaris	Leaf	CTM	Hermsen et al. (2007a)
Zamites spp.	Leaf	SVL	Plumstead (1962)
Conifer pollen cone	Pollen organ	CTM	Cantrill et al. (1995)

considered intraspecifically variable. The fossil woods from Skinner Ridge in this study are, therefore, assigned to *K. fremouwense*.

Antarcticoxylon priestleyi was established by Seward in 1914 based on a single piece of fossil wood collected from moraine debris on the Priestley Glacier, northern Victoria Land, in close vicinity to the Timber Peak fossil site (Bomfleur et al., 2007, 2011a). *Antarcticoxylon* shares significant features with *Kykloxylon* and *Rhexoxylon*, such as overall similar wood anatomy, the unusual occurrence of concentric bands of parenchyma, and the presence of sclerotic nests, and is therefore considered to belong to Corystospermales as well (Meyer-Berthaud et al., 1993). However, it has higher ray height (up to 24 cells), slightly larger primary xylem region, and secretory structures in the pith unlike *Kykloxylon*. Unfortunately, there is no information about its cross-field pit type. Due to the incomplete preservation and the uncertainty about the source strata of the single specimen, Mey.-Berth. et T.N.Taylor (1991; see also Meyer-Berthaud et al., 1993) have advised against the use of that name.

Jeffersonioxylon gordonense Del Fueyo, Ed.L.Taylor, T.N.Taylor et Cúneo (1995) was established based on fossil wood collected from the in situ fossil forest at Gordon Valley, Central Transantarctic Mountains. It was initially interpreted to be coniferous wood with affinities to Podocarpaceae (Del Fueyo et al., 1995). Subsequently, however, possible affiliation with Corystospermales has been suggested based on its conspicuous co-occurrence with *Dicroidium* leaf litter (Taylor et al., 1991, 2006; Taylor, 1996; Cúneo et al., 2003; Taylor and Taylor, 2009). Only recently, *Jeffersonioxylon* has been shown to be a junior synonym of *Kykloxylon* based on a detailed re-examination of the anatomy of the two taxa (Decombeix et al., 2014), and the type species, *J. gordonense*, was transferred to *Kykloxylon gordonense* (Decombeix et al., 2014). The specific differences between *K. fremouwense* and *K. gordonense* are few,

and the distinction is based mostly on the association with different *Dicroidium* species (Decombeix et al., 2014). Here, however, we consider *K. gordonense* to be a junior synonym of *K. fremouwense*, because they do share almost identical anatomical structure.

Notophytum krauselii Mey.-Berth. et T.N.Taylor (1991) is a fossil wood taxon for conifer stems reported from Fremouw Peak, Central Transantarctic Mountains. It differs clearly from our specimens and from corystosperm wood by the absence of unusual parenchymatous tissues, and by anatomical details of the pith.

Rudixylon serbetianum Bomfleur, Decombeix, Schwendemann, Escapa, Ed.L.Taylor, T.N.Taylor et McLoughlin (2014c) includes the very small stem fossils of the enigmatic gymnosperm group Petriellales T.N.Taylor, Del Fueyo et Ed.L.Taylor (1994). It can be distinguished easily from *Kykloxylon* by the different constituents in pith, i.e., the absence of the lacunae and sclerotic nests of *Rudixylon*. Based on comprehensive information of the morphology, anatomy, and taphonomical context, petriellalean plants in the high latitudes of Gondwana were interpreted as nanophanerophytes, which were shade-adapted perennial shrubs (Bomfleur et al., 2014c).

Rhexoxylon was established by Bancroft (1913) for stems of unknown age occurring in South Africa. Later, Walton (1923, 1925), Kräusel (1956), Archangelsky and Brett (1961), Brett (1968), Herbst and Lutz (1988), Taylor (1992), Artabe et al. (1999), and Bodnar (2008) reported *Rhexoxylon* species from South Africa, South America, and Antarctica. *Rhexoxylon* differs from *Kykloxylon* by the presence of centripetal growth, a wide pith (8–60 mm), peri-medullary bundles (except *R. cortaderitaense* Bodnar, 2008), and a smaller number (about 1–3) of large or small cross-field pits (Table 1). The *Rhexoxylon*-like stem reported by Taylor (1992) from Central Transantarctic Mountains

Table 3
List of research according to gymnosperm organ type for the Triassic of Antarctica.

Leaf	Reproductive organ		Wood		Root
	Ovulate organ	Pollen organ	Manoxylic wood	Pycnoxylic wood	
Plumstead (1962)	Perovich and Taylor (1989)	Osborn and Taylor (1993)	Smoot et al. (1985)	Seward (1914)	Millay et al. (1987)
Townrow (1967)	Yao et al. (1993)	Webb and Fielding (1993)	Hermsen et al. (2009)	Mey.-Berth. et T.N.Taylor (1991)	Hermsen et al. (2009)
Rigby and Schopf (1969)	Taylor et al. (1994)	Cantrill et al. (1995)		Meyer-Berthaud et al. (1992)	Decombeix et al. (2011)
Gabites (1985)	Axsmith et al. (1995)	Yao et al. (1995)		Taylor (1992)	
Rigby (1985)	Yao et al. (1997)	Axsmith et al. (2000)		Meyer-Berthaud et al. (1993)	
Tessensohn and Mädler (1987)	Axsmith et al. (2000)	Klavins et al. (2003)		Del Fueyo et al. (1995)	
Pigg (1990)	Klavins et al. (2002)	Hermsen et al. (2007b)		Cúneo et al. (2003)	
Taylor et al. (1990)	Decombeix et al. (2010b)	Bomfleur et al. (2011b)		Decombeix et al. (2014)	
Taylor et al. (1992)	Escapa et al. (2010)	Bomfleur et al. (2011c)		Bomfleur et al. (2014c)	
Boucher et al. (1993)	Schwendemann et al. (2010)	Chatterjee et al. (2013)		This study	
Webb and Fielding (1993)	Bomfleur et al. (2011b)				
Barale et al. (1994)	Bergene et al. (2013)				
Boucher et al. (1995)	Chatterjee et al. (2013)				
Axsmith et al. (1995)					
Cantrill et al. (1995)					
McLoughlin et al. (1997)					
Axsmith et al. (1998)					
Axsmith et al. (2000)					
Cúneo et al. (2003)					
Retallack (2005)					
Hermsen et al. (2006)					
Bomfleur et al. (2007)					
Hermsen et al. (2007a)					
Hermsen et al. (2009)					
Bomfleur and Kerp (2010)					
Bomfleur et al. (2011b)					
Bomfleur et al. (2011c)					
Escapa et al. (2011)					
Chatterjee et al. (2013)					
Bomfleur et al. (2014c)					

was recently suggested to be part of a *Kykloxylon* trunk rather than *Rhexoxylon* (Decombeix et al., 2010a, 2014).

Several other corystosperm wood types have been reported from South America, which is close to the Antarctic Peninsula: *Tranquiloxylon* R.Herbst et Lutz (1995), *Cuneumxylon* Artabe et Brea (2003), and *Elchaxylon* Artabe et Zamuner (2007) (Table 1). *Tranquiloxylon petriellai* R.Herbst et Lutz (1995), a monospecific genus, has some similarities to *Kykloxylon*, but differs in having a slightly larger pith, a continuous ring of primary xylem, and a peculiar leaf-trace structure. *Cuneumxylon* is another monospecific genus, reported from the Middle Triassic of the Paramillo Formation, Argentina, with the type species of *Cuneumxylon spallettii* Artabe et Brea (2003). This fossil wood taxon shares similar anatomical structures with large trunks of *K. fremouwense*, but the difference between the two taxa includes the presence of a much larger amount of parenchyma in radial and tangential directions in *Cuneumxylon* (Decombeix et al., 2014). The possibility of *Cuneumxylon* being junior synonym of *Kykloxylon* was thus suggested by Decombeix et al. (2014).

Elchaxylon zavattieriae Artabe et Zamuner (2007) is another corystosperm wood taxon, documented from the Upper Triassic Rio Blanco Formation, Argentina. It is distinguished easily from *Kykloxylon* by the presence of centripetal secondary xylem and of usually one or rarely two, three simple cross-field pits per field.

4. Discussion

Dense forest growth in Antarctica during the Triassic is amply documented by the abundance of wood fragments, large trunks, and large in situ trees in the Triassic deposits of the Beacon Supergroup throughout the Transantarctic Mountains (e.g., Jefferson and Taylor, 1983; Taylor and Taylor, 1993; Del Fueyo et al., 1995; Cúneo et al., 2003; Taylor and Ryberg, 2007; Decombeix et al., 2010a, 2014). Although the Triassic Antarctic forests were luxuriantly vegetated, the number of fossil wood taxa reported in Antarctica for this period is relatively low. Only four pycnoxylic wood species have been documented: *Antarcticoxylon*
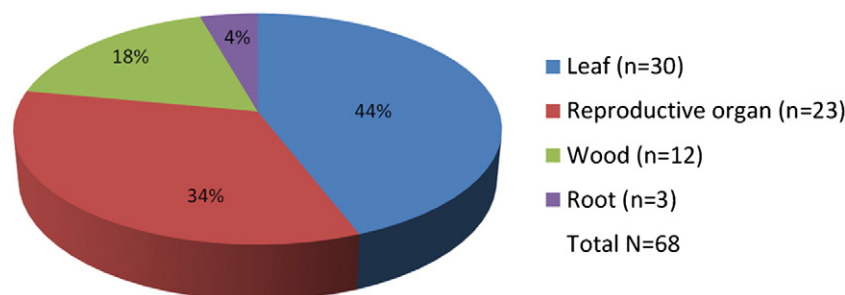
Fig. 4. A pie diagram showing the proportion of fossil plant studies according to the organ types.

priestleyi, *Kykloxylon fremouwense*, *Notophytum krauselii*, and *Rudixylon serbetianum* including the result of this study. By contrast, there is a much greater diversity in the fossil record of leaves and reproductive structures of seed plants (Table 2). Such a significant difference in diversity between wood and other seed plant fossils could have been caused by different chance of fossilization in different sedimentary condition. However, given the abundance existence of fossil woods including the *in situ* petrified forests as mentioned above, taphonomic process does not seem to be a major reason for the low wood diversity in Antarctica during the Triassic. Instead, we propose three major reasons for this relatively low wood diversity.

First, it might be due to the uniformity of gymnosperm wood. The secondary xylem of most Triassic gymnosperm wood consists of araucarioid-type pitted tracheids and ray parenchyma only, and is otherwise comparatively featureless. Extant gymnosperm woods are identified on the basis of their anatomical features, e.g., the seriation and arrangement of tracheid pitting in radial walls, the number and type of cross-field pits, the occurrence of helical and other wall thickenings in tracheids, the presence and arrangement of axial parenchyma, ray composition including the occurrence of ray tracheids and the thickening of ray cell walls, and occurrence of intercellular canals (IAWA Committee, 2004). Conversely, angiosperm woods have much more complicated anatomical structures and more diverse cell types (vessels, tracheids, fibers, axial and radial parenchyma, secretory canal, etc.), which build various patterns (IAWA Committee, 1989). The uniformity of Triassic gymnosperm wood-anatomical features could be one of the reasons why their apparent biological diversity is low, suggesting that several types of leaves or reproductive structures could have been produced by plants with a similar wood anatomy. Bamford (2004, p. 163) already suggested a similar reason to explain the lesser diversity of fossil wood assemblages than fossil leaf assemblages in the Permian–Triassic of southern Africa.

Secondly, the low apparent diversity could result from the sheer dominance of corystosperm plants with accessory voltzialean conifers during the Triassic in Antarctica. After the Permian, the glossopterid plants that dominated late Palaeozoic Gondwanan floras were substituted by corystosperm plants during the Triassic. According to Anderson et al. (1999), the corystosperms then constituted ca. 50% of the megafloral ratio in Gondwana floras and the proportion of conifers was lower than in both the Permian and Early Jurassic (Anderson et al., 1999). Although conifers did not dominate during the Triassic in Gondwana, one of the voltzialean conifers, i.e., *Notophytum*, was probably at least as ubiquitous as corystosperms in Antarctica (Mey.-Berth. et T.N.Taylor, 1991; see also Bomfleur et al., 2013). Other gymnosperms reported in Antarctica had manoxylic wood (e.g., cycads, Hermsen et al., 2009) or are reconstructed as plants of smaller stature (e.g., Petriellales, Bomfleur et al., 2014c) that did not produce large amounts of wood. So the corystospermous trees constituted the major canopy woody elements of the Triassic forests with a minor element of voltzialean conifers, *Nothophytum* in Antarctica, and this could explain the skewed pattern of wood diversity at that time.

Thirdly, there could be a bias caused by the fewer studies of fossil wood as compared to other megafloral elements for the Triassic. About 82% of studies carried out on Triassic gymnosperms focused on other plant organs (Table 3; Fig. 4). These differences in focus probably have several reasons, such as a collection bias because of the difficulty to identify various types of wood in the field and a smaller number of specialist fossil wood researchers to describe the collected specimens.

Other factors may also account for the low apparent diversity of Triassic woods. In particular, corystosperm-dominated vegetation in Antarctica during the Late Triassic might have been genuinely of low diversity. This low diversity might have concerned the whole ecosystem or only one vegetation stratum, for example the canopy, in which most arborescent woody species flourish. The latitudinal diversity gradient is a particularly striking feature of modern vegetation, with temperate forest tree species diversity being usually a tenth to a hundredth of that observed for wet tropical forests. There are no modern equivalents of Triassic subpolar forest, but if high boreal taiga is considered, it rarely features more than four genera dominance (McLaren and Turkington, 2013).

Since the first scientific record of fossil plants from Antarctica, which was a fossil wood from the South Shetland Islands (Eights, 1833), our knowledge about the biological evolution and vegetational changes in Antarctica has been vastly extended by the investigations of a wide variety of plants fossils, including fossil wood. However, there is still much to be discovered about the composition and functioning of Mesozoic polar forests, a type of ecosystem with no modern equivalent. Our on-going studies of Triassic plant fossils from Antarctica will hopefully contribute to a better understanding of plant growth and diversity under strongly seasonal conditions at high latitudes under a global greenhouse climate.

Acknowledgments

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